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Cone morphology in *Juniperus* in the light of cone evolution in Cupressaceae s.l.

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Summary

The interpretation of the berry-like, fleshy cones of *Juniperus* was up to now based on concepts about the conifer cone which are dismissed since Florin (1951). Comparative morphological and developmental studies showed that ovules alternating with the last whorl of cone scales cannot be regarded as part of a sporophyll (cone scale; pre-Florin interpretation). These alternating ovules are inserted directly on the cone axis and continue the phyllotactic pattern of the cone scales. If the usual seed scale is regarded as an axillary brachyblast (short-shoot) bearing ovules, the ovules alternating with ultimate whorls of cone scales in *Juniperus* sect. *Juniperus* can be regarded as a brachyblast terminating the cone axis. This interpretation allows to establish a standard bauplan for Cupressaceae in which species of *Cupressus* and *Juniperus* form a transition series towards more and more reduced cones. This series coincides with phylogenetic trees based on molecular studies.

Key words: *Juniperus*, Cupressaceae, cone, morphogenesis, ovule, evolution

Introduction

The fleshy, berry-like cones of *Juniperus communis* L. and other species of *Juniperus* sect. *Juniperus* (= sect. *Oxycedrus*) still pose a problem for taxonomists. Ovules alternating with cone scales like in *Juniperus* sect. *Juniperus* occur in *Microbiota* (Jagel & Stützel 2001b) and *Tetraclinis* (Jagel 2002, Jagel & Stützel in prep.) as well. Nevertheless, this exceptional position has been discussed in the past nearly exclusively for *Juniperus*. None of the different attempts to derive the *Juniperus* cone from a general conifer or even Cupressaceae pattern is really satisfying. The most frequent interpretation is the one represented by Eichler (1875) which was adopted directly or with modifications by Strasburger (1872), Renner (1907), Pilger (1926, 1931), Lemoine-Sebastian (1967), and numerous others (fig. 17B). In this concept, the ovules are formed by the cone scales of the ultimate whorl but not in median position. Some of the authors assumed an ancestor with the three cone scales bearing two ovules each. According to Strasburger (1872), adopted by Pilger (1926, 1931) and others, the loss of one of these ovules

should have led to a phylogenetic secondary shift of the remaining ovule into the gap between the scales. Herzfeld (1914) differs from this interpretation in assuming an ontogenetic shift (fig. 17A).

In developmental studies, such a shift was not detectable, and Schumann (1902) proposed an alternative model assuming an additional subtending bract for each ovule (fig. 17C). This interpretation would have brought in line the pattern of *Juniperus* with that known of other Cupressaceae. But Schumann noticed himself that the additional bract was not detectable in developmental studies either and thus regarded this interpretation as doubtful as the one by Strasburger (1872). It might be of some interest that both interpretations date back to the time when conifer cones where regarded as unbranched systems and the cone scales therefore were termed sporophylls. In the interpretation of the *Juniperus* cone, this outdated concept has survived, despite the fact that it has been abandoned since the studies by Florin (1951) in the early 50ths of the last century.

A third interpretation is the one by Sachs (1874), Kubart (1905), and Hagerup (1933). These authors regard the ovules in *Juniperus communis* and similar

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taxa as homologous to leaves (scales) because they take their position (fig. 17D). Despite having been proposed in regular intervals, this concept never found a broader acceptance, because in the classical spermatophyte concept ovules are megasporangia positioned somewhere on a megasporophyll. To homologize the ovule with an ovule bearing structure would imply a rejection of one of the basal axioms in spermatophyte evolution and is therefore mostly excluded from any considerations.

In a series of developmental studies in *Juniperus* and other Cupressaceae (Jagel 2002, Jagel & Stützel 2001a, 2001b), we tried to find the basic Cupressacean bauplan in which taxa like *Juniperus communis* and *Juniperus squamata* would fit as well. Taxa with a highly variable cone morphology like *Juniperus phoenicea* were supposed to provide additional data for the solution of this problem.

Materials and methods

Material was collected from April 2000 to April 2001. In the Botanical Garden of the Ruhr-University Bochum, collections were made twice a week except for the time of winter dormancy when collections were reduced to one per three weeks. The renewals with lateral branches of ultimate and subultimate order were fixed in FAA. At other places, collections were made when the dissections of material from BG Bochum suggested that essential developmental stages could be expected.

The following taxa were sampled: *Juniperus oxycedrus* L. subsp. *oxycedrus* (BG Bochum, SEM, CM), *Juniperus communis* L. subsp. *communis* 'Hibernica' (BG Bochum, BG Düsseldorf, BG Berlin-Dahlem, SEM), *Juniperus chinensis* L. 'Hetzii' (test field Ruhr-University Bochum, SEM, CM), *Juniperus chinensis* L. 'Sulphur Spray' (BG Düsseldorf, SEM), *Juniperus phoenicea* L. (BG Bochum, BG Düsseldorf, SEM), *Juniperus virginiana* L. (test field Ruhr-University Bochum, SEM), *Juniperus communis* L. var. *depressa* Pursh (BG Bochum, SEM), *Juniperus rigida* Siebold & Zucc. subsp. *conferta* (Parl.) Kitam. (BG Bochum, BG Düsseldorf, SEM), *Juniperus rigida* Siebold & Zucc. subsp. *rigida* (BG Bochum, BG Düsseldorf, SEM), *Juniperus sabina* L. (BG Düsseldorf, SEM), *Juniperus squamata* Buch.-Ham. ex D. Don (BG Bochum, SEM, CM); BG = Botanical Garden, CM = complete morphogenesis, SEM = scanning electron microscopy.

After one week of fixation in FAA, the samples were transferred and stored in ethanol (70%). The first dissection steps were carried out in ethanol, final dissection was usually done after Critical-Point-Drying. Critical-Point-Drying was done according to Gerstberger & Leins (1978). Dehydration in FDA was extended to 24 hours. Sputter coating was done with a Balzers SCD 050, SEM studies were done with a Zeiss DSM 950 supplemented with a Digital Imaging System (DIS) supplied by Electronic Point.

The species were determined using the diagnostic keys by Dallimore & Jackson (1966), Krüssmann (1983), Mitchell (1972), and Farjon (1992). In addition, descriptions from Engelmann (1878), Britton (1923), Cory (1936), Munz & Keck (1959), Rechinger (1968), Kerfoot & Lavranos (1984), Hart & Price (1990), Roloff & Bärtels (1996) were used. Taxonomy and nomenclature follow Farjon (2001). Cone diagrams were drawn in analogy to the floral diagrams introduced by Eichler (1875).

Results

Sect. *Juniperus* (*J. communis, J. oxycedrus, J. rigida*)

The first developmental stages of *Juniperus* berry-cones were found in August. At this stage, reproductive buds can hardly be distinguished from vegetative buds and are only slightly thicker than vegetative ones. The ovular primordia are ovoid and slightly radially elongated (fig. 1A, B), while cone scale primordia are transverse elliptical. The entire process of ovule development (fig. 1) takes about 2–3 weeks.

Among 128 cones (*Juniperus communis* and *Juniperus oxycedrus)* dissected or analysed under the dissecting microscope, 25 abnormal cones were found. In two cones the apex elongated to a narrow tip (fig. 2C), in one cone a terminal ovule occurred instead of this tip (fig. 2D). In one cone a second whorl of ovules alternated with the first whorl (fig. 2E, the second whorl of ovules marked with asterisks). This ultimate whorl was situated in the centre of the cone. The three ovules did explicitly not develop in the axils of the ultimate whorl of cone scales. One of the ovules of the outer whorl was not completely developed. At a size where ovules have already a clearly differentiated integument, it had a shape which is typical to early stages in leaf development. Some cones seemed to be rather irregular (fig. 2B, 8B) but can be understood as variants of the cone in fig. 2A and fig. 8A by converting ovules into more or less leaf-like intermediate structures. Rarely ovules abort in an early developmental stage (fig. 8C) or ovules occur in the axils of the subultimate whorl of cone scales in addition to the non axillary ovules (fig. 8D). At pollination time, the tips of micropyles are conspicuously exserted in the cone (fig. 2F), so that the pollination droplets remain separated and cannot form a joined "superdroplet", as often occurs in *Cupressus* (Jagel & Stützel 2001a).

Fig. 1. *Juniperus oxycedrus;* cone development, left side top view, right side same object in lateral view. A, B initiation of the ovular whorl; the radial prolongation makes the primordia clearly distinguishable from transversely prolongated leaf primordia. C, D after formation of the integument, micropylar region slightly bent outwards. E, F shortly before pollination time. cs = cone scale, i = integument, n = nucellus, o = ovule, op = ovule primordium.
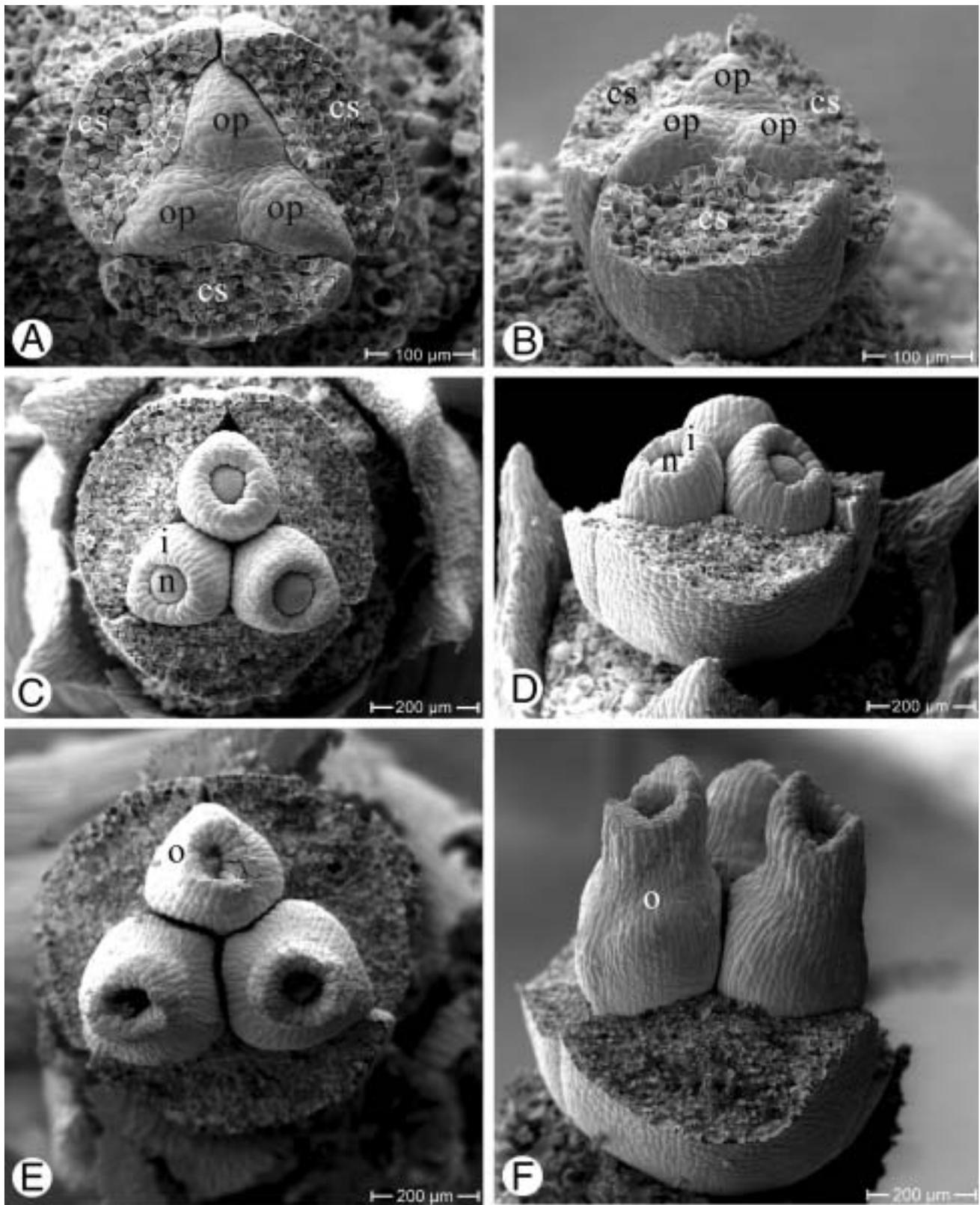
Fig. 1
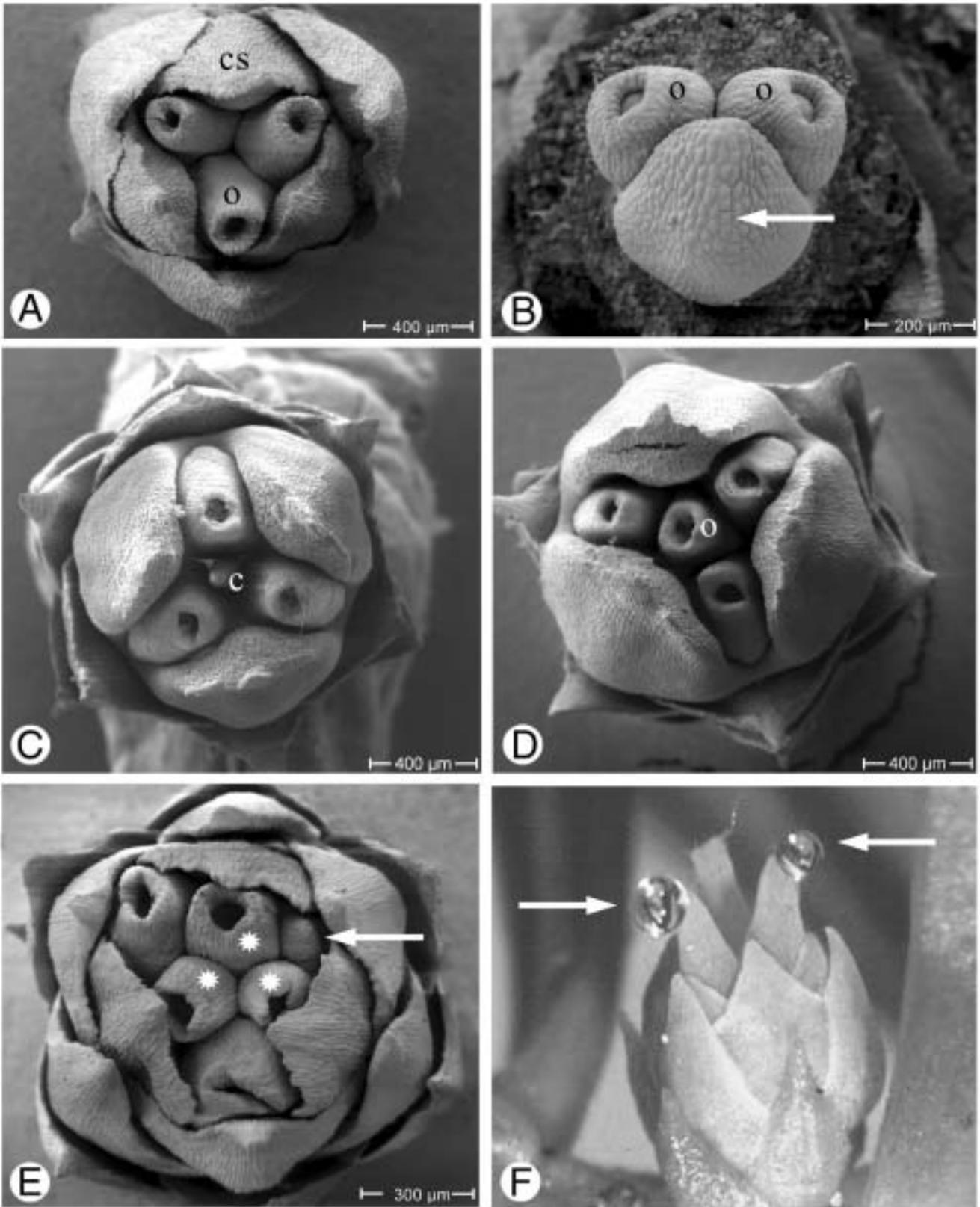
Fig. 2

Juniperus squamata

Juniperus squamata usually develops one single ovule in the centre of the cone (fig. 4). While the vegetative apex is conically shaped (fig. 3 A, B), the beginning of the ovule formation in mid June can be recognized by the apex becoming flat (fig. 3 C, D). A cylindrical ovular primordium emerges at this flat apex with the upper margin becoming more and more prominent (fig. 3 E, F). At the beginning of July, the integument starts to separate from the nucellus as a shallow rim (fig. 4 A, B), more and more enveloping the nucellus (fig. 4 C, D). The ovule becomes triangular, its ribs alternating with the cone scales of the preceding whorl (fig. 4 E, 9 A). The "berry" is formed by a basal, ventral swelling of each cone scale of the ultimate whorl. The swellings fuse in later stages to form a ring around the ovule (fig. 4 F).

Sometimes the branches show decussate phyllotaxis instead of trimerous whorls. In this case, decussate cones occur, followed by an ovule with only two ribs (fig. 5 A, 9 B). Rarely a two-ribbed ovule occurs in a trimerous cone (fig. 5 B, 9 D). While normally the ovule primordium is mostly placed exactly in the centre of the cone suggesting that it takes the place of the cone apex (fig. 5 C), it sometimes is slightly shifted towards one of the scales (fig. 5 D) or towards the gap between two scales (fig. 5 E, 9 C). The shift might be the effect of a slightly plagiotrophic orientation of the reproductive branch, but this could hardly be proved. As different slightly eccentric positions occur, this is most likely an effect of this kind, rather than an indication for an axillary or alternating position of the ovule, and a terminal position of the ovule is most likely the general pattern.

After pollination, the micropylar channel is closed by protruding and dividing cells from the inner surface of the micropyle (fig. 5 F). A similar development is known from other Cupressaceae and *Cephalotaxus* (own studies, unpublished) as well as e.g. from *Taxus*, (STRASBURGER 1904).

Fig. 2. A–E: *Juniperus communis;* A, normal cone in top view. B, cone in which in one ovule the differentiation into nucellus and integument did not take place, so that an intermediate structure between ovule and leaf was formed (arrow). C, cone with an elongated sterile cone axis. D, cone with an additional ovule terminating the cone axis. E, nearly regular cone, in which distal to the normally present ovules a second whorl alternating with the first one follows; one of the ovules of the typically developed whorl is degenerated and resembles a leaf primordium (arrow). F, *Juniperus rigida* subsp. *conferta*, cone at pollination time, exserted micropyles prevent a fusion of the pollination droplets. cs = cone scale, o = ovule, c = columella.

Juniperus chinensis

The typical cone of *Juniperus chinensis* has decussate cone scales and bears two ovules (fig. 10 A). The development of the cones starts in May. Each cone scale of the subultimate whorl develops an axillary meristem (fig. 6 A, B), which forms usually a single ovule. In this cone type the ultimate whorl of cone scales remains sterile. In early stages, the ovules sometimes seem to be positioned laterally to the median plane (fig. 6 C – E). In older stages, this asymmetry disappears and the ovule seems to be more or less perfectly in the median plane (fig. 6 F). In late developmental stages (fig. 6 F), it might be difficult to distinguish between a position in the axils of the subultimate whorl of cone scales and a position following the ultimate whorl and alternating with it.

In some cones, instead of a single axillary ovule in median position two ovules occur symmetrically to the

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Fig. 3. *Juniperus squamata;* A, vegetative apex in top view. B, same specimen as in A in lateral view; the vegetative apex is characterized by the conically shape. C, early stage of the development of the terminal ovule. D, same specimen as in C in lateral view, the apex is slightly larger and much flatter than the vegetative one. E, ovule primordium slightly older than in C and D; the shape is more or less truncated coniform. F, same specimen as in E in lateral view. a = apex, csp = cone scale primordium, cs = cone scale, op = ovule primordium.

Fig. 4. *Juniperus squamata;* A, first stages of the formation of the integument. B, same specimen as in A in lateral view. C, terminal ovule after the formation of the integument. D, same specimen as C in lateral view. E, ovule at about pollination time. F, formation of the fleshy leaf bases as a ring around the ovule (arrow) after pollination time. cs = cone scale, n = nucellus, i = integument, o = ovule, r = rib.

Fig. 5. A–E *Juniperus squamata;* A, ovule with two ribs following a dimerous whorl of cone scales; B, ovule with two ribs following a trimerous whorl of cone scales. C, terminal position of the ovular primordium in a dimerous cone. D, eccentric ovular position with shift towards a cone scale. E, ovule in slightly eccentric position shifted towards the gap between two cone scales; F, closure of the micropylar channel after pollination time. c = cells, csp = cone scale primordium, mc = micropyle canal, i = integument, op = ovule primordium, r = rib.

Fig. 6. *Juniperus chinensis;* A, the first stages of ovule development are indicated by the formation of a meristem (arrow) in the axils of the subultimate whorl of cone scales. B same specimen as in A in lateral view. C, D, E, later stages of ovule development with slightly eccentric position (arrow). F, later developmental stages do not show the eccentric position, asymmetric growth seems to lead to more or less perfect median position of the ovule. cs = cone scale, op = ovule primordium.
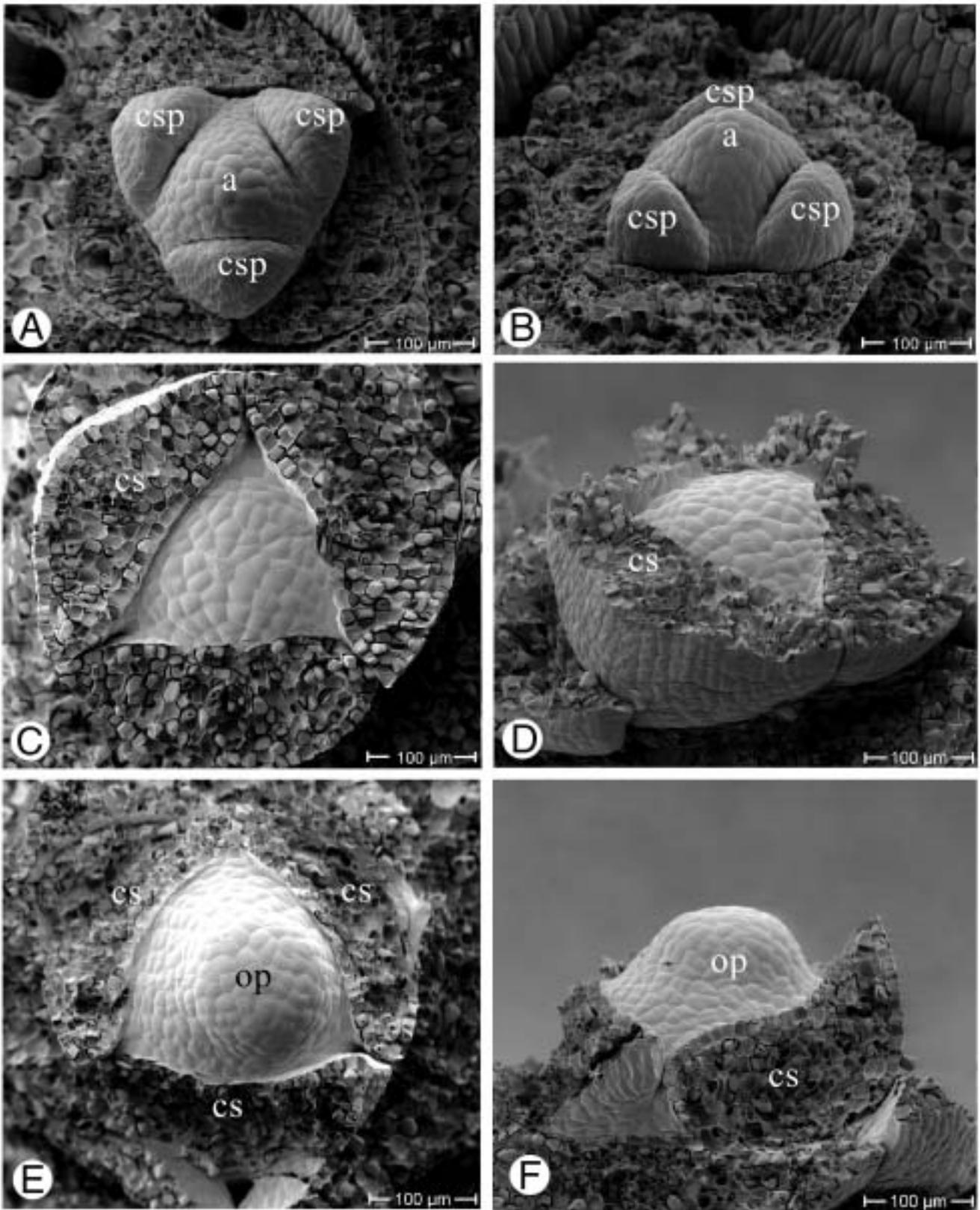
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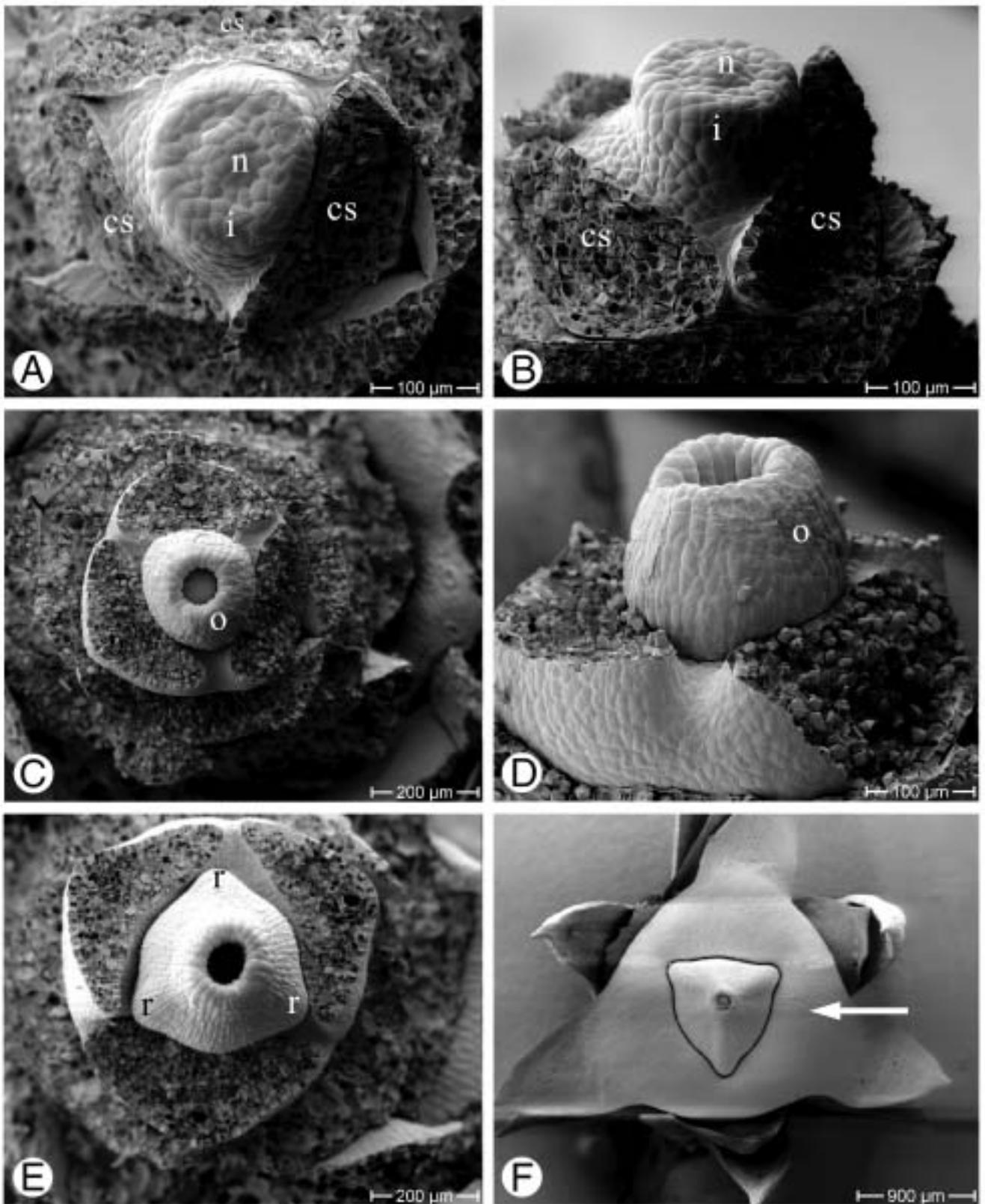
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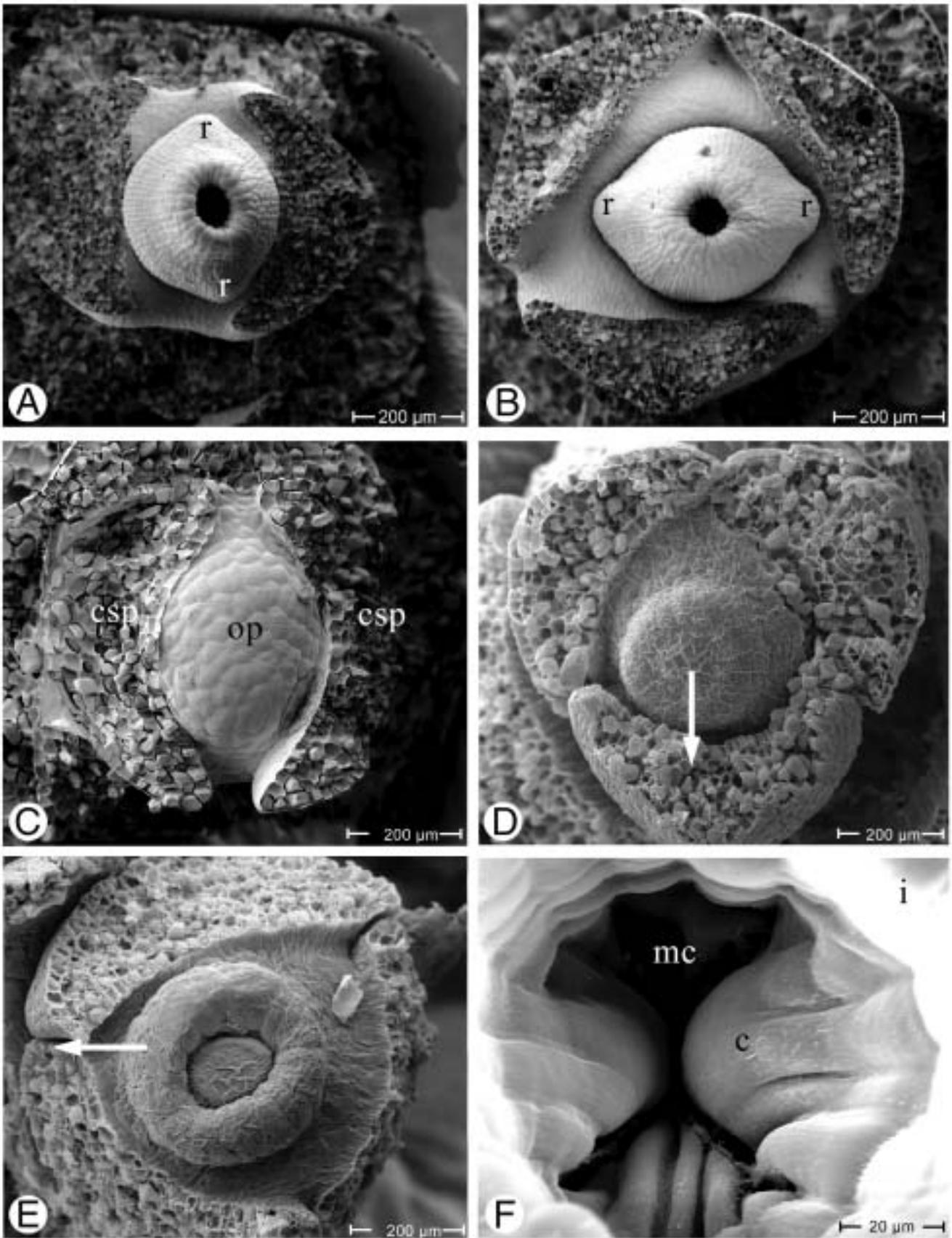
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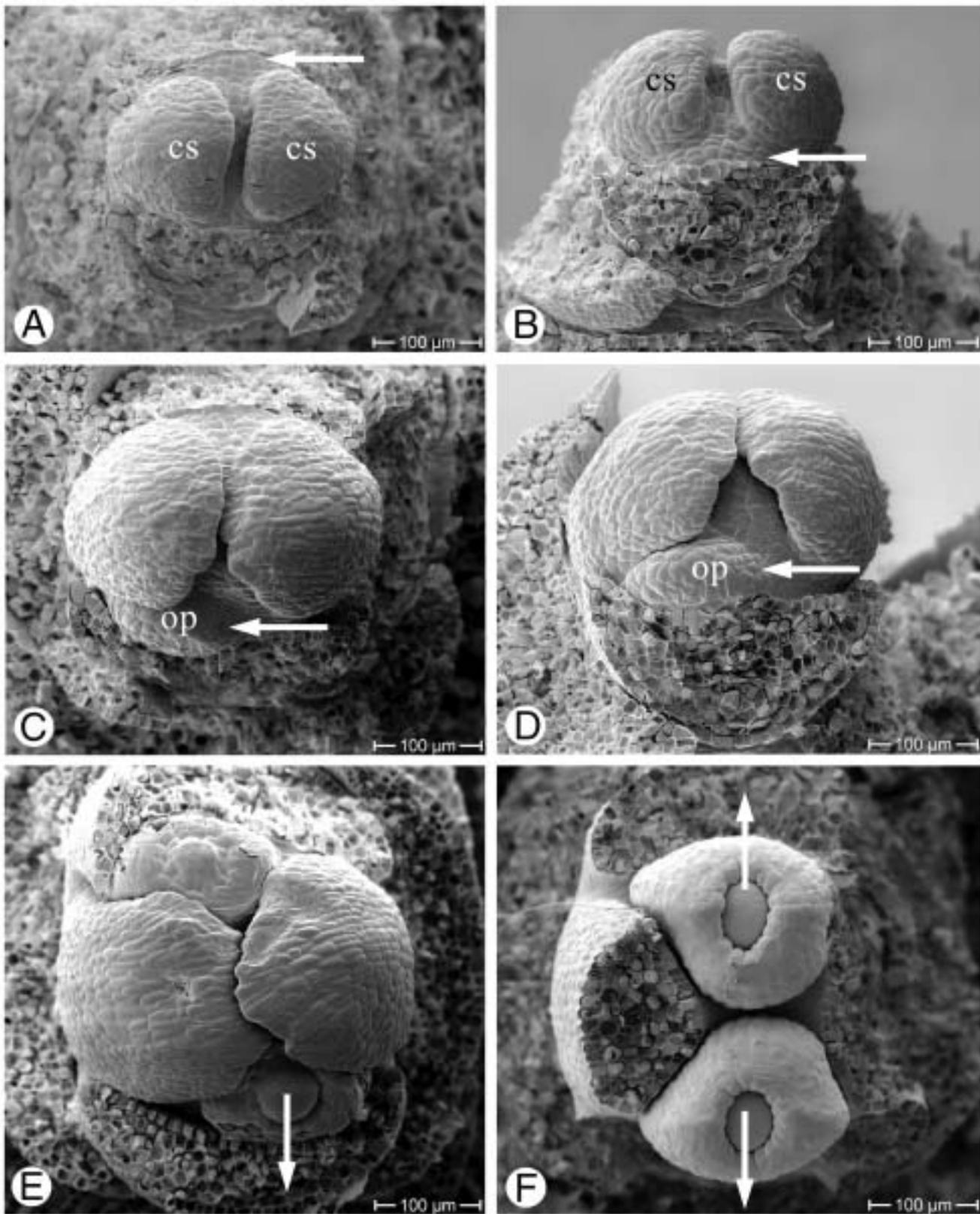
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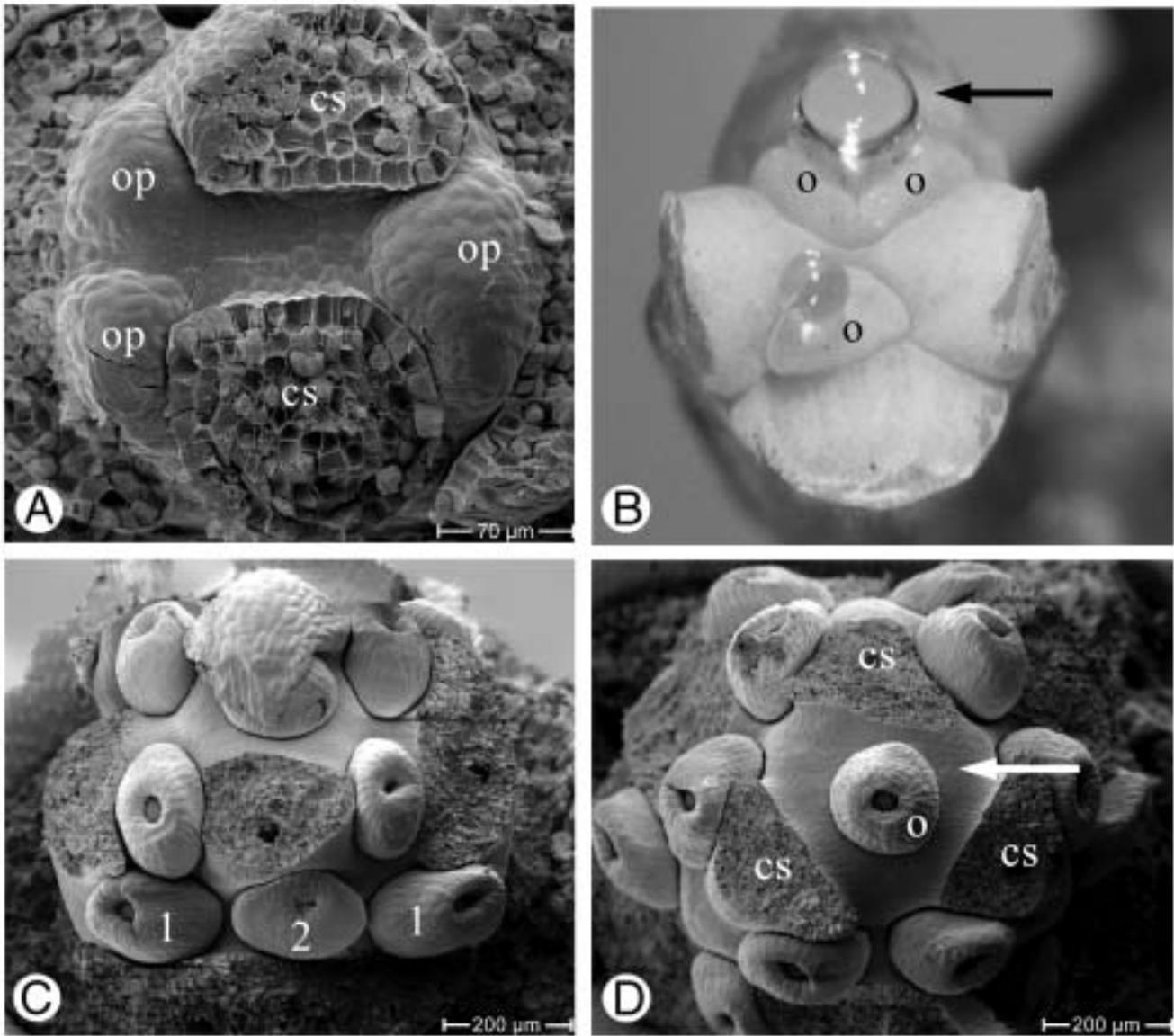
Fig. 7. A–B, *Juniperus chinensis;* A, the meristem on the left side has divided into two ovular primordia which are much smaller than the single median one on the right side. B, paired ovules may form fused oversized pollination droplets (arrow). C–D, *Juniperus phoenicea*. C, dimerous cone, lower whorl of cone scales bearing three ovules, the following whorl with two ovules per scale, uppermost whorls sterile, one single ovule terminating the cone axis (partially covered by one of the ultimate cone scales, which was not removed). D, trimerous cone with two symmetrically arranged ovules in the axil of each scale and a single ovule terminating the cone axis (arrow). cs = cone scales, o = ovule, op = ovule primordium.

median plane (fig. 10B). Sometimes only in the axil of one cone scale of the facing scales two primordia are born (fig. 7A). In this case, the paired primordia are much smaller than the unpaired one in the axil of the facing scale. In the mature cone, no or only minor size differences between single and paired ovules can be seen if both paired ovules finish their development, but frequently one of the two paired ovules aborts at an early developmental stage. Some cone types bear ovules, which develop evidently in terminal position (fig. 10A,

D). In paired ovules, the pollination drops tend to fuse to a joined and extremely large droplet (fig. 7B).

Juniperus phoenicea

Juniperus phoenicea displays the widest range in cone morphology within the investigated taxa (see also Far-jon & Ortiz Garcia 2002). Therefore, it is difficult to give an entire developmental series for "the cone of
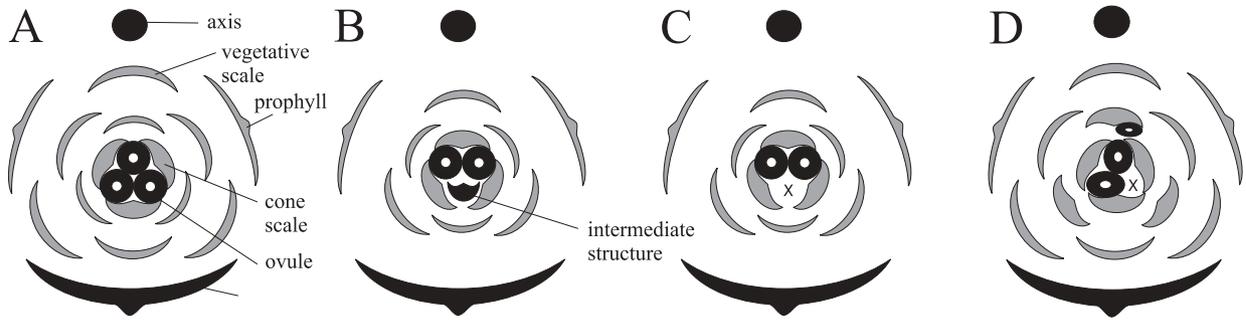
Fig. 8. *Juniperus oxycedrus*, cone diagrams. A, typical diagram. B–D, exceptional and rare diagram. B, with transitional structure between ovule and leaf. C–D, with aborted ovules. D with an additional ovule in the axil of a subultimate scale.
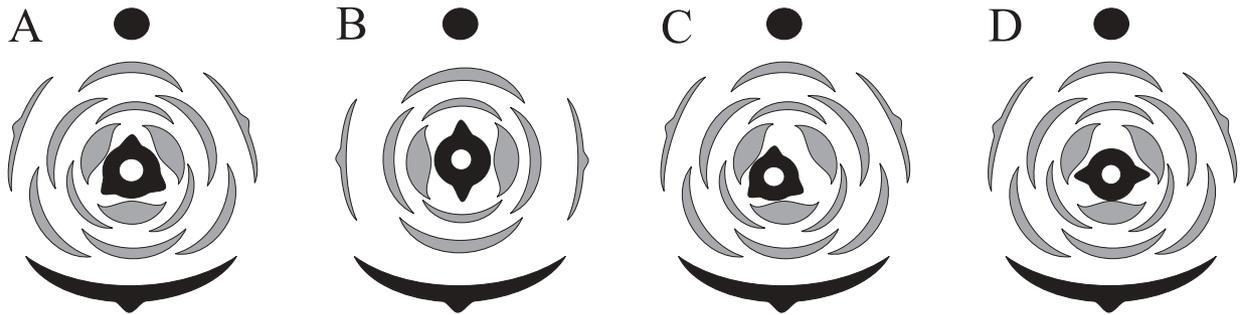
Fig. 9. *Juniperus squamata*, cone diagrams. A, B typical trimerous and dimerous diagram. C, trimerous diagram with eccentric position of the ovule. D, trimerous diagram with a two-ribbed ovule.
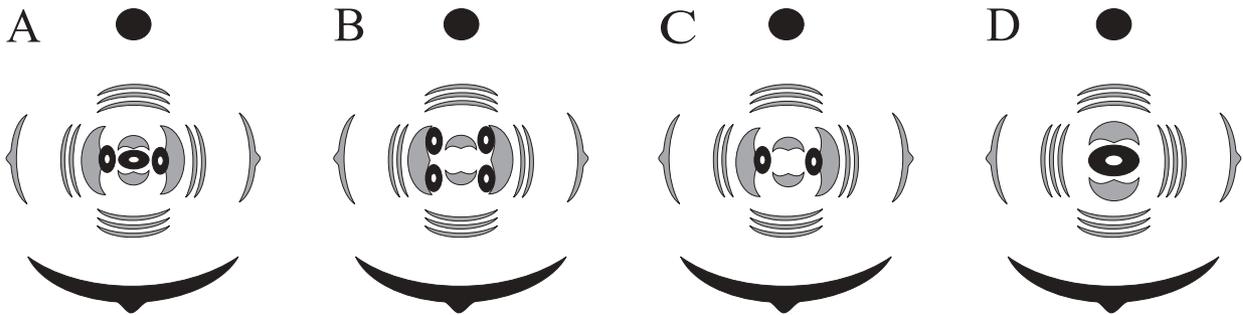
Fig. 10. *Juniperus chinensis*, cone diagrams. Ovules may be solitary in medium position to the cone scales (A, C), paired in the axil of the scale (B) or terminal to the cone axis (A, D). No one of these diagrams is significantly predominant.
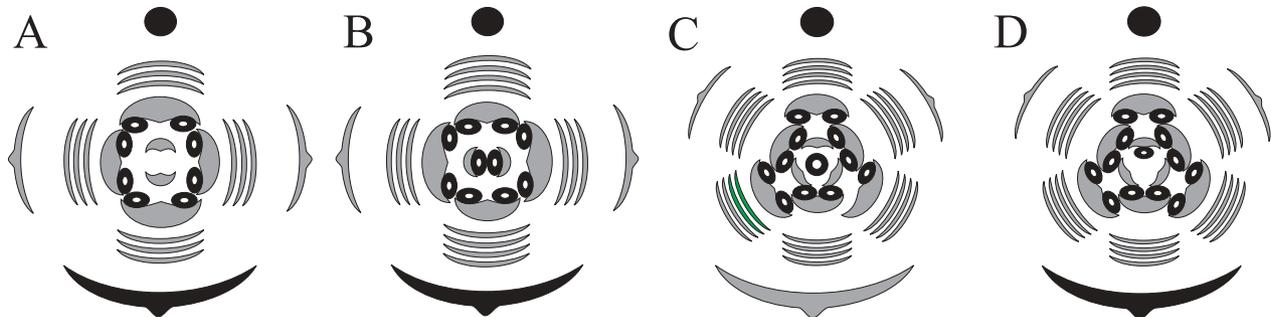
Fig. 11. *Juniperus phoenicea*, cone diagrams of dimerous (A, B) or trimerous (C, D) cones with more than a single whorl of fertile scales. Single ovules may occur in medium position to the cone scale (B, D) or terminal to the cone axis (C).

J. phoenicea". The samples studied are stages leading to different mature cones and cannot be composed to a single developmental sequence as it can be done rather easily in taxa with only little variability. The variations comprise a) the number of whorls (2–4), b) the number of ovules per fertile scale (1–3), c) trimerous versus dimerous cone scales, and d) presence or absence of ovules distal to the ultimate whorl of scales including terminal ovules. About 30 different arrangements of scales and ovules have been found (some examples are shown in fig. 11). Nevertheless, some general patterns could be detected. The lowermost fertile scales tend to bear more ovules than the distal ones. The ovules are generally arranged symmetrically to the median plane, e.g. three ovules with one in median position (fig. 7C), two ovules with the median one absent or aborted (fig. 7D), or a single median ovule only (fig. 11 B, ultimate whorl). Additional ovules in terminal position may occur as well (fig. 7D, arrow). Asymmetric arrangements are obviously the effect of abortions which take place after initiation of a symmetric arrangement during the development. As a result, such arrangements can be found more frequently in mature cones and at pollination time than in early developmental stages.

Discussion

Coinciding positions in molecular trees (Gadek & Quinn 1993; Gadek et al. 2000) as well as combined morphological and molecular analysis (Gadek et al. 2000) and careful morphological studies (Jagel & Stützel 2001b; Farjon & Ortiz Garcia 2002) indicate that small cones, and especially small cones with exceptional ovular position, have to be regarded as derived from larger ones with many cone scales and sterile cone scales at the distal end of the cone. In our opinion, the primitive cone is therefore similar to what can be found today in genera like *Sequoia, Sequoiadendron* or *Metasequoia*. Cones with extreme numbers of ovules per scale and up to four rows of ovules per scale are derived from the ancestral cone type as well as extremely reduced cones like those of *Juniperus* and *Microbiota*. However, *Juniperus* is not closely related to *Microbiota*.

The facts known to date give equal support to all concepts mentioned in the introduction, but do not allow to exclude one of them definitely. As the arguments for or against the different models are substantially based on general concepts in gymnosperm evolution, it cannot be expected that the solution results from studies restricted to *Juniperus communis* or even to the genus *Juniperus* as a whole. It is therefore essential to analyse the existing data for Cupressaceae s.l. (incl. Taxodiaceae) for general patterns which could be extrapolated towards the morphological features of *Juniperus*. These general patterns can be detected best in cones with many fertile scales, many ovules and several rows of ovules per scale as it is realized in *Cupressus*. *Cupressus* shows the bauplan of Cupressaceae in its most complete and elaborate form and is therefore crucial for its understanding. However, this does not imply that *Cupressus* displays the type closest to the ancestors of recent Cupressaceae.

The cones of *Cupressus* show several patterns which are relevant for the question under consideration here (Jagel & Stützel 2001a; Jagel 2002). The cone scales develop in acropetal sequence and the axillary products (seed scales) of the fertile scales do as well. Some scales at the distal end of the cone may remain sterile or not. As the earliest fossil records of Cupressaceae are *Cunninghamia*-like species (Stewart 1990) with sterile scales at the distal end, one might assume that this is the ancestral state within Cupressaceae s.l. This is supported by the fact that taxodioid Cupressaceae are regarded as basal within Cupressaceae, based on morphological evidence as well as on molecular data. The ovules in the axil of a cone scale are arranged in one to several rows. The rows are always formed in a centrifugal (= basipetal) sequence and the ovules within a row in a centripetal sequence (Jagel 2002, Farjon & Ortiz Garcia 2003).

The centripetal formation within a single row seemed to be disputable for a long time for different reasons. On the one hand, some ovules may abort in different and even relatively early developmental stages, and these abortions obviously do not follow a regular pattern. Studies based on material at pollination time or even older stages are therefore often misleading. On the other hand, the genus *Chamaecyparis* seems to display a single row of ovules with a definite centrifugal initiation sequence. However, Jagel & Stützel (2001a) have shown that this phenomenon is caused by a developmental pattern unique to *Chamaecyparis*. In this genus, up to three rows (perhaps up to four, see Li 1972) of ovules are formed, each row normally consisting of merely two ovules. As the ovules of the outer (basal) rows appear lateral to the preceding ones, the basipetal sequence of the different rows appears as a centrifugal formation of a single row (fig. 12, curved double arrow). Exceptional cases with three or four ovules per row indicate that this interpretation is correct (fig. 12, smaller ovules). This basic pattern has been demonstrated by Jagel (2002) for all Cupressaceae studied to date.

The pattern in *Juniperus phoenicea* is similar to what Jagel & Stützel (2001b) described for *Platycladus orientalis*. The approach of classical morphologists to derive the different ovule arrangements from the "most complete pattern" (3 ovules) just by a stepwise omission of ovules (fig. 13A) would lead to a single ovule in eccentric position. But the reduction does not follow this

typological way. In the axil a broad meristematic band is formed, which is then divided into parts (fig. 13B). The dividing process starts from the margins. If the band is broad enough, three ovules are formed. If it is not broad enough, either a small rudiment remains in median position or only two ovules without median rudiment are formed. If the meristematic band is more narrow, either two congenitally fused ovules, or a single ovule with two nucelli, or a single oversized median ovule may appear (see JAGEL & STÜTZEL 2001a, b), the normal result is a single median ovule. Simplistic morphological interpretations may be misleading, and if the developmental process is taken into consideration, the centripetal formation sequence of the ovules within a single row seems to be well established for *Juniperus phoenicea* as well.

Juniperus chinensis seems to have given some investigators problems of interpretation because of a rather frequent somewhat eccentric position of a single ovule. STRASBURGER (1872) might have used aspects of ovule arrangements like in fig. 6C–E as an argument for his "ovule-shifting concept". But the paired primordia (fig. 7A, left side) are so much smaller than the unpaired ones (fig. 7A right side), that one might easily assume that they are close to a situation where they are too small to develop further towards mature ovules. Furthermore, according to the "ovule-shifting concept", these eccentric ovules should move more towards the gap between the leaves in their further development. But in fact there seems to be a shift to the median position instead (fig. 6F). This is difficult to detect as we cannot study the development of a single cone, but we can reconstruct it from stages of different age of different cones. In taxa with high developmental variability and various types of

Fig. 13. A, stepwise omission of ovules leads to the concept of an asymmetric (lateral) position of a single ovule; asterisk = lacking ovule. B, the assumption of a gradual reduction of the size of the axillary meristem (grey areas) leads to a median position of a single ovule as it can be observed in many Cupressaceae; dot = rudiment or lacking ovule.

mature cones, classical developmental studies may lead to ambiguous or unclear results. But the developmental stages we have found indicate that single ovules in the axil of the bract are shifted into median position and never into a position alternating with cone scales.

The interpretation by STRASBURGER (1872) and followers has therefore to be rejected. The reason is not that such a shift is not detectable, but that the developmental pattern on which STRASBURGER's concept is based does occur neither in *Juniperus* nor in other members of Cupressaceae. If there is only a single ovule, it is always in median and not in lateral position. Occasional lateral ovules are the result of an early abortion of one of two (rarely two of three) symmetrically initiated ovules.

The second relevant process is a shift of the fertile zone of cone scales towards the distal end of the cone (fig. 14). In *Sequoia, Cunninghamia, Chamaecyparis, Fokienia* and others, there are always some sterile scales at the distal end of the cone (fig. 14A). In comparison to the more proximal ones the ultimate fertile cone scales bear a generally reduced number of ovules. Within *Cupressus* and *Juniperus* sect. *Sabina* a shift of the fertile zone towards the distal end of the cone can be detected (fig. 14B, C). First, all distal scales become fertile (fig. 14C), then the number of fertile scales is reduced, so that only two or three fertile whorls at the distal end remain. But in these taxa, the axillary origin of the ovules remains clear. The only exception is *Fitzroya*, where three glands are formed alternating to the ultimate whorl of scales. These glands thus have the same position in the bauplan as the ovules in *Juniperus communis* and are sometimes regarded as aborted ovules (SAHNI & SINGH 1931), sometimes as reduced scales. They are formed later than the preceding scales and even later than the ovules in the axils of the preceding scales (JAGEL 2002), which could be an indication that the

Fig. 12. Ovule initiation in *Chamaecyparis*: the up to 6 ovules seem to form one single row with centrifugal initiation sequence (curved double arrow). Abnormal cones with additional ovules (drawn in smaller size) indicate, that the axillar group of ovules is formed of up to three rows of ovules which comprise 2 or rarely 3 ovules each (the rows marked by dotted line). The general cupressacean developmental pattern (centripetal within a row, centrifugal (basipetal) from row to row) applies therefore for *Chamaecyparis* as well.

Fig. 14. Morphological transition series within Cupressoideae cones based on cone morphology. The fertile zone is shifted towards the cone apex (A–C) and finally a terminal brachyblast (short-shoot) in addition to fertile scales (D) or only a fertile brachyblast (E) is formed. Cha = *Chamaecyparis*, Cup = *Cupressus*, Fok = *Fokienia hodginsii*, Jun = *Juniperus* sect. *Juniperus*, Sab = *Juniperus* sect. *Sabina*, Tet = *Tetraclinis articulata*, Tho = *Thujopsis dolabrata*, Thu = *Thuja*.

glands do not represent ovule equivalents (JAGEL & STÜTZEL, in prep.).

One of the difficulties in interpretating the cones in Cupressaceae is the question of what has to be regarded as the "ovuliferous scale" (seed scale). Additional confusion results from the fact that "ovuliferous scale" is sometimes used as a synonym of "seed scale" and "fruit scale", sometimes the latter two describe different structures. In this case, the term "fruit scale" means only the stalk of an individual ovule (for details see MUNDRY 2000; CLEMENT-WESTERHOF in BECK 1988). This explains, while seemingly conflicting descriptions for well-known structures are still in use.

In most Cupressaceae s. str. (not in taxodioid Cupressaceae; following FARJON 2001 *Sciadopitys* is excluded from Taxodiaceae and therefore from Cupressaceae s.l. as well), there is no flattened and in the widest sense leaf-like structure at all. Thus, cones of this group of Cupressaceae are often described as "without ovuliferous scale". Others regard the whole axillary complex including all ovules as the "seed scale", and thus according those authors all Cupressaceae have a seed scale by definition. According to SCHWEITZER (pers. communication), this applies especially for some palaeobotanists.

In a fairly descriptive way, one can say that the ovules in the axil of a cone scale form together an axillary brachyblast (short-shoot). If there is more than a single row of ovules per axil, the subsequent rows can be re-

garded as accessory brachyblasts (JAGEL 2002). As accessory brachyblasts are common as first renewals in *Metasequoia* and probably some other taxodioid Cupressaceae, this interpretation is not as unlikely as it
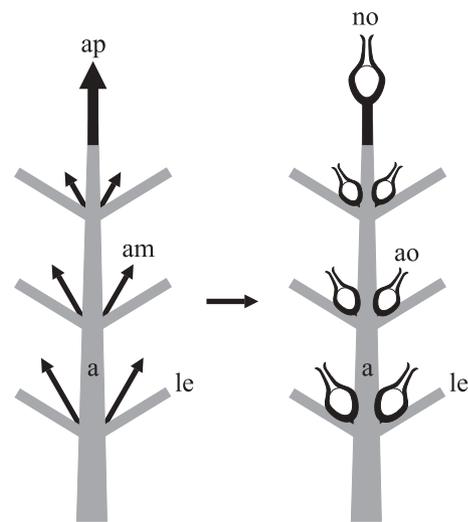
Fig. 15. Different development of ovules. The non-axillary ovules develop from apical meristem and axillary ovules from axillar meristem. a = axis, am = axillar meristem, ao = axillary ovules, ap = apical meristem, le = leaf, no = non-axillary ovules.
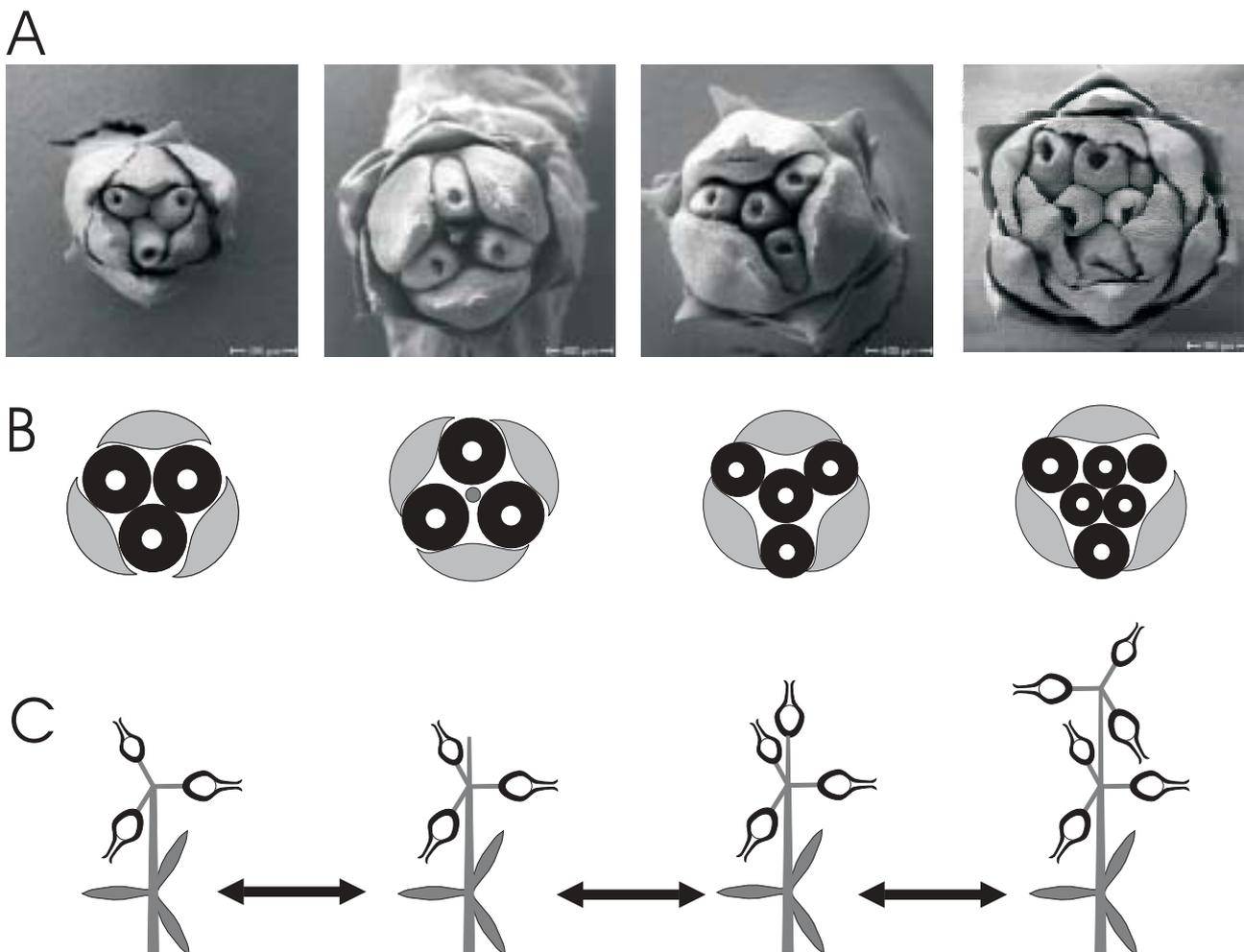
Fig. 16. Cones in *Juniperus communis* in A: top view, B: diagram and C: the interpretation of the pattern suggested here (in lateral view).

might seem at first glance. In conifers as well as in many angiosperm groups with a short-shoot / long-shoot differentiation, we can find brachyblasts continuing their growth as long-shoots and on the other hand long-shoots being terminated by a brachyblast in terminal position. In the same way a cone may terminate the vegetative long-shoot in *Taxodium*. It does not matter in this context, that some authors regard the female cones as long-shoots themselves. The cone as a structure of limited growth, which normally is placed on a lateral axis, may in weakly growing branches terminate the relative main axis as well. One of the many examples in angiosperms is *Pyrus*, where the flowering brachyblast may terminate a long-shoot of the previous year. In *Pyrus* long-shoots and terminating short-shoots develop in subsequent years and are separated by bud scales from each other. If the same occurs sylleptically in one single year, the indicative bud scales are lacking.

If one supposes that in *Juniperus communis* and other members of sect. *Juniperus* a "seed scale" (a reproductive brachyblast bearing ovules) is formed in a terminal position to the cone axis, this would give an explanation for the cone morphology of sect. *Juniperus* which would be consistent with the patterns and tendencies realized in Cupressaceae cones. Such a terminal "seed scale" or ovuliferous scale would have lateral ovules continuing the phyllotactic pattern of the long-shoot in one or more whorls of ovules (fig. 14D, E), and may have only, or in addition, an ovule terminating the scale and in this case at the same time the cone axis (fig. 15). The interpretation of different cone types of *Juniperus* sect. *Juniperus* is shown in fig. 16.

Such a concept has some affinities to the widely ignored or even rejected concept by SACHS (1874), KUBART (1905) and HAGERUP (1933) (fig. 17D). In fact, it would also easily explain the intermediate structures
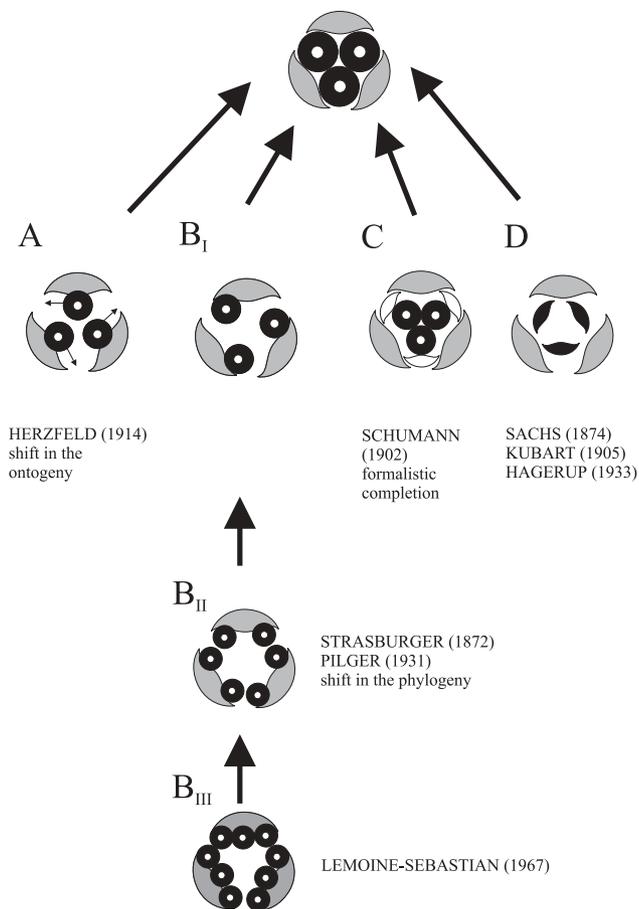
Fig. 17. Historical interpretations of the *Juniperus* sect. *Juniperus* cone. B is the one accepted generally hitherto in some variants.

between leaves (cone scales) and ovules, which occur frequently but not regularly instead of ovules in normal cones and cones with additional ovules (fig. 2B). The position of such intermediate structures should not be irregular intermixed with ovules and scales, but they have to be expected at the borderline between scales and ovules as intermediates. In addition, similar structures may terminate the cone axis, where they represent aborted ovules (fig 2C). There is no final proof for our interpretation, but our concept is at least much better than the one by STRASBURGER (1872) and successors which clearly failed in the context of a general Cupressaceae bauplan, while our concept is consistent with it.

We would not go as far as concluding that the ovules are homologous to leaves. But we think that up to now there is no serious evidence for any kind of "sporophyll" in true conifers. The three dimensional arrangement of telomes leading to megasporangium and integument according to the model proposed by ANDREWS (1961) can hardly be brought in line with the two dimensional arrangement of telomes in a leaf. On the other hand there are intermediate structures between leaves and ovules in *Juniperus*. These intermediates include intermediate developmental stages as well as intermediate mature stages. The meaning of such structures is yet completely unclear.

The puzzling situation is that we found a new interpretation for the cone of *Juniperus communis* which fits perfectly in a general bauplan for Cupressaceae, but which raises new problems in respect to the evolution of the ovule. Further studies have to show, if the described intermediate structures are really intermediate or not. These studies have to include data from fossil records as well. In the meantime, the concept of a terminal seed scale and the intermediates between ovules and leaves may also be a subject for studies in developmental genetics, which may deliver proofs or counterevidence for the model presented here.

Acknowledgements

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